



Is the introduction of novel exotic forest tree species a rational response to rapid environmental change? – A British perspective



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ABSTRACT

Both plantation forests and native woodlands are currently facing challenges in the form of rapid climatic change and unprecedented increases in damage by exotic pests and diseases. To combat these problems it has been proposed that a range of novel exotic tree species (non-native species that have not yet undergone thorough operational testing or previously been grown at a forestry scale) should be grown as part of an adaptive management strategy, and that non-native (including novel) species should be introduced into native woodland. Justifications for this policy are that novel exotic species are required to maintain forest productivity under climate change, to create a more diverse, and by implication more resilient forest, and to substitute for native species threatened by introduced pests and pathogens. Here we examine these arguments in the context of British forestry, where there is a long history of utilising non-native species. On the basis of this documented experience we conclude that in the commercial sector of British forestry, where production is the main objective, there are strong arguments for undertaking a programme of rigorous testing and domestication of a very limited number of the most promising novel exotics which, in addition to good timber and growth, also have attributes that will allow the development of more naturalistic silvicultural systems and a move away from current clear-fell regimes. However this must be undertaken within a comprehensive risk assessment framework, where candidate species are rigorously screened both for any biosecurity threats, and their potential for causing ecological damage if they become invasive outside their initial planting sites. Widespread planting of candidate species should only be recommended after the completion of full species and provenance trials, and when reliable sources of appropriately adapted seed have been established. Conversely where conservation of biodiversity is an objective we find no support for introduction of any non-native species. This is based on the greater ecological and economic risk they pose compared to the use of native species. Use of non-natives is likely to lead to an increase rather than a decrease in pest and disease problems, and to hinder rather than support the retention of threatened native tree species and their associated biodiversity.

1. Introduction

The environment experienced by forest tree species is changing very rapidly, largely as a result of human activity. Anthropogenic rise in greenhouse gases is driving complex changes in the mean and variability of climatic parameters, whose future values cannot be predicted with great certainty (IPCC, 2014). These climatic changes will have direct effects not only on the trees themselves, but also on their associated organisms (Walther, 2010). At the same time large scale movements of species around the globe, both in international trade, and as a consequence of the establishment of exotic plantations, are

homogenising global biodiversity (Olden et al., 2004). This is exposing forest trees to novel pests and pathogens that have the power to inflict severe economic and ecological damage in an unpredictable way (Brasier, 2008; Santini et al., 2013; Ennos, 2015; Ghelardini et al., 2016; Budde et al., 2016).

Currently there is vigorous debate about the adaptive forest management policies that should be developed in response to the simultaneous challenges posed by climate change and the rise in exotic pests and pathogens. One proposal involves the introduction, into both plantations and semi-natural forests, of novel exotic tree species, defined here as non-native species that have not yet undergone thorough

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operational testing or previously been grown at a forestry scale (Thorpe et al., 2006; Meason and Mason, 2014; Felton et al., 2013; Kjær et al., 2013, 2014). In this paper we set out the arguments for utilising such novel exotic species as a component of our adaptive forestry response to rapid environmental change. We then assess the commercial risks of adopting this strategy, and the wider ecological impacts that it may have. To provide a real world context for our analysis we focus on forestry in Britain, where there has been encouragement to include novel exotics within a broader mix of species as part of a strategy to adapt forests to climate change and increase their resilience (Natural Resources Wales, 2017; Forestry Commission England, 2018a,b,c,d; Forest Research, 2018a). A detailed appraisal of this situation is particularly pertinent because British foresters already have a long history of utilising exotic tree species (MacDonald et al., 1957; Lines, 1987; Malcolm, 1997).

2. The British forestry context

Forestry in Britain encompasses a range of management objectives, often pursued in close geographic proximity or even within the same stands (Forestry Commission, 2017). These range from intensive timber production, through multipurpose forestry sustaining a variety of ecological and social benefits, to conservation of native woodlands and their associated biodiversity. Scots pine (*Pinus sylvestris* L.), the sole commercially important indigenous conifer, shows good growth over a wide area but is unsuitable on the wetter sites available for much of commercial forestry in northern Britain. The timber production sector in Britain is therefore heavily reliant on exotic tree species. Norway spruce (*Picea abies* L.) was introduced as early as the sixteenth century, while European and Japanese larch (*Larix decidua* Mill. and *L. kaempferi* (Lamb.) Carrière) were eighteenth and nineteenth century introductions (Anderson, 1967) respectively. All three species are now well-established in British forestry (Anderson, 1967). These have been joined by a number of exotic conifers indigenous to NW America that were introduced earlier but were only subjected to intensive trialling in Britain from the 1920s (Malcolm, 1997). The productive conifer sector is now dominated by Sitka spruce (*Picea sitchensis* (Bong.) Carrière), which constitutes 52% of all conifer plantations and has proved adaptable to a wide range of site types (Kerr et al., 2015c). Scots pine stands comprise 17% of conifer planting but there are also significant areas of the following exotics; lodgepole pine (*Pinus contorta* Douglas ex Loudon) (10%), larch (5%), Norway spruce (5%), Corsican pine (*Pinus nigra* J.F. Arnold subsp. *laricio* (Poir.) Maire) (2%), and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) (2%) with a small contribution from species such as grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western red cedar (*Thuja plicata* Donn ex D. Don) (Kerr et al., 2015c). All of these species have been extensively tested over a long period and are regularly used in commercial forestry. We refer to these as well-established exotics to distinguish them from the novel exotics with which this paper is chiefly concerned.

At the other end of the British forestry management spectrum lie the native woodlands where the major objective is conservation of native woodland communities, the native trees therein, and their associated biodiversity (Peterken, 1977). Native woods range from the Caledonian Scots pinewoods (Mason et al., 2004) to a diversity of broadleaved woodland types where species such as oak (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.), ash (*Fraxinus excelsior* L.) and birch (*Betula pendula* Roth and *B. pubescens* Ehrh.) are widely important. The native distribution of woods dominated by beech (*Fagus sylvatica* L.) is restricted to southern Britain (Forestry Commission, 2003). Native woods may also contain a proportion of well-established exotic broadleaves such as sycamore (*Acer pseudoplatanus* L.). Native woodlands are typically highly fragmented and have been heavily modified by past management, overgrazing and exploitation, which has often severely reduced the diversity of tree species that they contain (Anderson, 1967;

Côté et al., 2004; Watts, 2006). Many of these native woodlands, whether formerly managed for timber or not, are currently showing signs of neglect.

Between these two extremes lie woodlands managed for multiple purposes. These may have their origins in exotic conifer plantations that have been restructured to fulfil objectives other than timber production, or native woodlands where indigenous species may be managed for timber production and within which there may be significant plantations of the well-established exotic species mentioned above, yielding timber returns.

The patchwork of forest types in the British landscape and the different objectives for which they are managed means that actions taken in one forestry sector are likely to have an impact on all other forestry sectors. It is therefore important to consider jointly the effects of novel exotic introductions on timber production in commercial forestry, ecosystem services and social provision in multipurpose forests, and biodiversity conservation in native woodlands.

3. Arguments supporting the introduction of novel exotic species in Britain

In this section we set out the diversity of arguments that make the case for introduction of novel exotic species into Britain's forests.

3.1. Maintaining forest productivity under climate change

Climate change modelling for Britain predicts 2.5–3 °C warming over the period to 2100, and changes in seasonal rainfall distribution leading to an increase in frequency and intensity of summer droughts in the east, particularly the south-east of England (Broadmeadow et al., 2009; Ray et al., 2010; Met Office, 2011). To assess the impact of such climate change on British forests, the ecological site classification (ESC) model (Pyatt et al., 2001) has been used. This relies on empirical measurements of the performance of important forest tree species across different environments to predict their productivity under a variety of anticipated scenarios. Inputs to ESC are the values of four climatic (accumulated temperature, moisture deficit, exposure and continentality) and two edaphic (soil fertility and wetness) factors at a site. The model returns the predicted productivity of a candidate species at the site, relative to its maximum possible productivity in Britain under present conditions. Five productivity bands are defined, ranging from > 70% of maximum possible productivity (very suitable) to < 30% (unsuitable). ESC model projections indicate that over the next century, productivity in the north and west of the UK will increase for many native and well-established exotic species. However a number of commercially important taxa including Sitka spruce are predicted to show significant reductions in timber production by 2080 caused by drought stress, particularly in the east of the country (Broadmeadow et al., 2009). The conclusions drawn from application of the ESC model are supported by independent predictions from process based models of tree growth (Landsberg et al., 2003; Coops and Waring, 2011). These also indicate that warmer and drier climates will lead to significant reductions in productivity of Britain's most important timber producing species Sitka spruce (Meason and Mason, 2014), especially in eastern areas where growth is already commercially marginal due to damage under summer drought (Green et al., 2008; Green and Ray, 2009).

In response to these predictions, a breeding programme to select for more drought tolerant Sitka spruce genotypes could be set up, or Sitka spruce could be replaced on marginal sites by a more drought tolerant species. Given the long lead in time, substantial investment and uncertainty associated with delivering Sitka spruce genotypes with improved drought tolerance, species replacement provides the best short-term solution (Lee and Connolly, 2010). Native or well-established exotic species could be employed as a replacement (e.g. Scots pine or Douglas fir) (Cameron, 2015; Meason and Mason, 2014). Another strategy would be to introduce novel exotics with desirable drought

tolerance attributes. Candidate species that have been suggested include; oriental spruce (*Picea orientalis* (L.) Peterm.) (Mason et al., 2012), Macedonian pine (*Pinus peuce* Griseb.) and coast redwood (*Sequoia sempervirens* (D.Don) Endl.) (Ray et al., 2015).

In southern Britain, where timber production is more focused on species other than Sitka spruce, it has also been argued that productivity can only be maintained if species whose growth is likely to suffer under projected climate change are replaced with drought adapted species in future plantings (Ray et al., 2010). For instance, the growth rate of beech is anticipated to be unacceptably low by 2080 especially on sites with poor water retention capacity. Replacement with well-tried timber producing species such as native hornbeam (*Carpinus betulus* L.) and the long-established exotic sweet chestnut (*Castanea sativa* Mill.) is an option. Alternatively, a novel exotic with high drought tolerance could be used as suggested by Ray et al. (2010). However the species they originally proposed, Roble beech (*(Nothofagus) Lophozonia obliqua* (Mirb.) Heenan & Smissen), has since been ruled out due to its vulnerability to *Phytophthora pseudosyringae* (T. Jung and T.I. Burgess, 2009).

3.2. Increasing resilience of forests

Britain's productive forest industry is dominated by a single exotic species, Sitka spruce, grown in monocultures over a wide range of site types under a patch clear-fell silvicultural regime (Malcolm, 1997). The species has been the subject of an intensive tree improvement programme such that a significant proportion of trees currently being planted are from a limited number of half or full-sib families that have been clonally propagated, potentially narrowing the genetic base substantially in these production stands (Lee and Watt, 2012; Conifer Breeding Co-operative, 2017). Lack of genetic, species and structural diversity in plantations leaves the species, and by implication the British forest industry, exposed to very high risk both from extreme climatic events, whose frequency is set to increase in the future, and from introduction of exotic pests and diseases specific to spruce. This situation has stimulated a major policy initiative to increase the diversity of productive plantations both in terms of structure and species composition to reduce their exposure to risk (Forestry Commission, 2017).

As indicated earlier, British foresters already have extensive experience with growing a range of other well-established exotic conifers which could be used to diversify Sitka spruce plantations (Cameron, 2015). However each of these has limitations in terms of site requirements, vulnerability to herbivores, unacceptable wood quality, etc. (Wilson, 2011). Therefore there is considerable interest in introducing a new suite of exotic species with attributes that will facilitate diversification (Kerr et al., 2015c). One such attribute is shade tolerance which is required to allow development of continuous cover systems that can deliver structural diversity (Kerr, 1999). At least seven novel exotic conifers, for which varying levels of experience are available in Britain (summarised in Forest Research (2018b)), are being considered to achieve diversification of spruce plantations (Table 1). They comprise Pacific silver fir (*Abies amabilis*) Douglas ex J. Forbes), European silver fir (*Abies alba* Mill.), Serbian spruce (*Picea omorika* (Pančić) Purk.), white spruce (*Picea glauca* (Moench) Voss), Macedonian pine, coast redwood and Japanese red cedar (*Cryptomeria japonica* (L.f.) D.Don) (Wilson, 2011).

The perception of vulnerability due to low species diversity within and between stands, and at the landscape level, though most visible in the timber production sector, is also present in policy related to less intensively managed multipurpose woodlands. The fact that Great Britain is a relatively small island, with a recent glacial history, means that native tree diversity is naturally low (Ingrouille, 1995). Past management and excessive grazing have further reduced tree species diversity in many multipurpose and conservation woodlands (Côté et al., 2004), potentially increasing their vulnerability to extreme

climate episodes or introduction of new pests and pathogens. Therefore a major theme evident in the Forestry Standard that guides sustainable forestry in Britain, is that species diversity of multipurpose and conservation woodlands should be increased to enhance their resilience to environmental change (Forestry Commission, 2017; Bellamy et al., 2018). The underlying rationale is that overall risk is lower in a more species diverse forest because that risk is spread among more species.

The default position is that diversification should be achieved using native species and well-established exotics (Forestry Commission, 2017). However in England and Wales there is considerable interest in broadening the palette of species planted in multipurpose woodlands by incorporating novel exotics in the mix with native species. Among the total list of candidate species suggested for effecting diversification there are 32 (England) and 23 (Wales) novel exotic tree species (Table 1) (Forest Enterprise England, 2018a, b; Forestry Commission England, 2018a; Natural Resources Wales, 2017). To facilitate their future use, relevant background information on the distribution, ecology, possible seed sources and silviculture of these species has been made available (Forest Research, 2018b; Silvifuture, 2018). In Scotland emphasis is primarily on the use of native and well-established exotic species to increase species diversity (Grant et al., 2012). Indeed following the passing of the Wildlife and Natural Environment (Scotland) Act (2011) it is an offence in Scotland to plant non-native trees in forestry unless they appear on a list of 'exempt' species (Forestry Commission Scotland, 2015). While most 'exempt' species are well established exotics, 19 of these taxa nevertheless fall into the category of novel exotics (Table 1).

3.3. Retaining biodiversity associated with threatened native species

Over the last 50 years there has been an exponential increase in epidemics of introduced exotic tree pests and pathogens in Europe (Santini et al., 2013). In Britain 4 of the 36 native tree species (two species of elm (*Ulmus minor* Mill. and *U. glabra* Huds.), ash and Scots pine) have been, and continue to be, seriously affected by introductions of Dutch elm disease (*Ophiostoma novo-ulmi* Brasier 1991), ash dieback (*Hymenoscyphus fraxineus* Baral et al. (2014) and Dothistroma needle blight (*Dothistroma septosporum* (Dorog.) Morelet) respectively (Brown and Webber, 2008; Gibbs, 1978; Gross et al., 2014a). Demise of a native tree species has a huge impact on biodiversity both as a consequence of structural changes in the habitat affecting understorey plants, and the loss of associated species directly dependent upon the tree for their existence.

In native woodlands, where maintenance of biodiversity is a priority, a possible adaptive response for mitigating the loss of an indigenous tree species caused by an exotic pest or pathogen, is to introduce a closely related exotic species or 'functional analogue' that is resistant to the pest or pathogen, yet occupies the same niche and is capable of supporting a large proportion of the community of organisms associated with the native tree (Broome and Mitchell, 2017; Buggs, 2012). Using the same logic but over a longer timescale, it has been proposed that if we anticipate the demise of particular native tree species under projected climate change scenarios, it may be possible proactively to introduce closely related relatives or 'functional analogues' capable of surviving under future climatic conditions in order to support biodiversity associated with the native species after it has been lost (Stone, 2013).

4. Analysis of the arguments supporting introduction of novel exotic species in Britain

In this section we examine the arguments put forward above to support the introduction of novel exotic tree species into Britain. Recognising the diversity of objectives in British forestry, our analysis deals separately with forests at either end of the management spectrum; those managed for timber production, and those managed for

Table 1

Novel exotic tree species being considered for introduction into British forestry. * - Species specifically proposed for commercial conifer diversification. 1 and 2 – Species proposed for climate change adaptation and diversification by Forestry Commission England and Forestry Commission Wales respectively. 3 – Species given exemption from planting restrictions in Scotland under the Wildlife and Environment Act (Scotland) 2011. Other columns indicate presence or absence of data from species trials (ST) and provenance trials (PT) and existence of certified seed sources (SS) in Britain. Also shown are known biosecurity and adaptation problems, related species present in Britain, shade tolerance of the novel species, and tree species already present in Britain with which the novel exotics could hybridise.

Species	ST	PT	SS	Existing biosecurity/adaptive problems	Related Species in British Forests	Shade tolerance	Hybridises with:
Broadleaves							
<i>Acer macrophyllum</i> 1, 2	No	No	No	<i>Phytophthora ramorum</i>	<i>Acer pseudoplatanus</i>	Intermediate	
<i>Acer saccharinum</i> 1	No	No	No	<i>Ceratocystis virescens</i>	<i>Acer pseudoplatanus</i>	Intermediate	
<i>Alnus viridis</i> 1	No	No	No	<i>Phytophthora alni</i>	<i>Alnus glutinosa</i>	Intermediate	
<i>Alnus incana</i> 1, 2, 3	No	No	No	<i>Phytophthora alni</i>	<i>Alnus glutinosa</i>	Low	<i>Alnus glutinosa</i>
<i>Alnus cordata</i> 1, 2	No	No	No	<i>Phytophthora alni</i>	<i>Alnus glutinosa</i>	Low	
<i>Alnus rubra</i> 1, 2, 3	Yes	No	No	<i>Phytophthora alni</i>	<i>Alnus glutinosa</i>	Low	
<i>Eucalyptus gunnii</i> 1, 2	No	No	No	Low frost tolerance		Low	
<i>Eucalyptus nitens</i> 1, 2	No	No	No	Low frost tolerance		Low	
<i>Liriodendron tulipifera</i> 1	No	No	No	<i>Phytophthora ramorum</i>		Low	
<i>Nothofagus pumilio</i> 1	No	No	No	<i>Phytophthora pseudosyringae</i>		Low	
<i>Nothofagus alpina</i> 1, 2, 3	No	No	No	<i>Phytophthora pseudosyringae</i>		Low	
<i>Nothofagus obliqua</i> 1, 2, 3	No	No	No	<i>Phytophthora pseudosyringae</i>		Low	
<i>Paulownia tomentosa</i> 1	No	No	No			Low	
<i>Populus alba</i> 3	No	No	No	<i>Melampsora larici-populina</i>	<i>Populus tremula</i> <i>Populus nigra</i>	Low	<i>Populus tremula</i>
<i>Populus tremula</i> × <i>Populus tremuloides</i> 3	No	No	No	<i>Xanthomonas populi</i>	<i>Populus tremula</i> <i>Populus nigra</i>	Low	<i>Populus tremula</i>
<i>Populus trichocarpa</i> 1, 2	No	No	No	<i>Melampsora larici-populina</i>	<i>Populus tremula</i> <i>Populus nigra</i>	Low	<i>Populus nigra</i>
<i>Populus nigra</i> × <i>Populus deltoides</i> 1, 2	No	No	No	<i>Melampsora larici-populina</i>	<i>Populus tremula</i> <i>Populus nigra</i>	Low	<i>Populus nigra</i>
<i>Populus alba</i> × <i>Populus tremula</i> 3	No	No	No	<i>Melampsora larici-populina</i>	<i>Populus tremula</i> <i>Populus nigra</i>		<i>Populus tremula</i>
<i>Populus deltoides</i> × <i>Populus trichocarpa</i> 1, 2	No	No	No	<i>Melampsora larici-populina</i>		Low	
<i>Quercus rubra</i> 1, 2, 3	No	No	No	<i>Phytophthora ramorum</i>	<i>Quercus robur</i> <i>Quercus petraea</i>	Low	<i>Populus nigra</i>
Conifers							
<i>Abies nordmanniana</i> *, 1, 2	No	No	No	<i>Dreyfusi nusslini</i>	<i>Abies grandis</i>	High	
<i>Abies alba</i> *, 1, 2, 3	Yes	Yes	No	<i>Dreyfusi nusslini</i>	<i>Abies grandis</i>	High	
<i>Abies amabilis</i> *, 1, 2, 3	Yes	Yes	No	<i>Heterobasidion annosum</i>	<i>Abies grandis</i>	High	
<i>Cedrus atlantica</i> 1, 3	No	No	No	<i>Sirococcus tsugae</i>	<i>Tsuga heterophylla</i>	Low	
<i>Cedrus deodar</i> 3	No	No	No	<i>Sirococcus tsugae</i>	<i>Tsuga heterophylla</i>	Low	
<i>Cedrus libani</i> 1, 3	No	No	No	<i>Sirococcus tsugae</i>	<i>Tsuga heterophylla</i>	Low	
<i>Cryptomeria japonica</i> *, 1, 2, 3	No	No	No			High	
<i>Metasequoia glyptostroboides</i> 1	No	No	No			Low	
<i>Picea glauca</i> × <i>Picea sitchensis</i> *	Yes	Yes	No		<i>Picea sitchensis</i> <i>Picea abies</i>	High	<i>Picea sitchensis</i>
<i>Picea orientalis</i> 1, 2	No	No	No	<i>Dendroctonus micans</i>	<i>Picea sitchensis</i> <i>Picea abies</i>	Intermediate	<i>Picea sitchensis</i>
<i>Picea omorika</i> *, 1, 2, 3	No	No	No		<i>Picea sitchensis</i> <i>Picea abies</i>	Intermediate	
<i>Pinus mugo</i> 3	Yes	No	No	<i>Dothistroma septosporum</i>	<i>Pinus sylvestris</i>	Low	
<i>Pinus muricata</i> 3	No	No	No	<i>Dothistroma septosporum</i>	<i>Pinus sylvestris</i>	Low	
<i>Pinus peuce</i> *, 1, 2, 3	No	No	No			Low	
<i>Pinus pinaster</i> 1	No	No	No	<i>Dothistroma septosporum</i>	<i>Pinus sylvestris</i>	Low	
<i>Pinus radiata</i> 1, 2	No	No	No	<i>Dothistroma septosporum</i>	<i>Pinus sylvestris</i>	Low	
<i>Pinus monticola</i> 1, 2	No	No	No	<i>Cronartium ribicola</i>		Intermediate	
<i>Pinus strobus</i> 1, 2	No	No	No	<i>Cronartium ribicola</i>		Intermediate	
<i>Sequoia sempervirens</i> *, 1, 2, 3	No	No	No	Low frost tolerance		High	
<i>Sequoiadendron giganteum</i> 1, 3	No	No	No			Low	

conservation.

4.1. Maintaining viable forests under climate change

4.1.1. Forests managed for timber production

In those British forests managed for timber production that are likely to experience an increase in the frequency of damaging summer droughts under climate change, there is an overwhelming need and logical argument for replacement of species whose productivity is projected to fall significantly over the next century (Ray et al., 2010). These species include Sitka spruce in north-eastern Britain, and beech in south-eastern England. There are also very powerful arguments for diversifying silvicultural systems away from clear fell monoculture based on Sitka spruce which, as we have outlined in section 3.2, is particularly

vulnerable to damage by both extreme climatic events and introduced exotic pests and pathogens. Given the requirement for species change, the next question to consider is whether replacement species should be drawn from the pool of native and well-established exotic species, or from a potentially wider list of novel exotics. Such a decision requires an appreciation of the additional commercial risk associated with the use of novel exotic species. The magnitude of this additional risk can be ascertained by drawing on experience from historical exotic introduction programmes.

In Britain and elsewhere, exotic species have been successfully integrated into commercial forestry on the basis of knowledge and experience gained from thorough, lengthy and costly research programmes (Burdon, 2001; Lines, 1987; Zobel et al., 1987). These begin with comprehensive species trials over the full range of site conditions

to identify the environments in which the candidate species is capable of productive growth. Replicated provenance experiments of those species that show promise are then set up to identify seed origins that are appropriately adapted to British conditions. Finally seed stands or orchards for generating suitable planting stock are established. Once this programme has been completed, robust, evidence based recommendations can be made for large scale planting from appropriately adapted seed sources (Lines, 1987). Thus after extensive provenance testing of Sitka spruce in Britain, seed origins from Queen Charlotte Islands were shown to be the best adapted to British conditions, with some potential for growing Washington origins in the southwest (Lines, 1987).

In contrast any immediate use of novel exotic species, by definition, will be on the basis of far less evidence, commonly the results of assessment of single or very low numbers of individuals growing in arboreta, demonstration plantings or preliminary, rather than comprehensive, species trials. This brings with it appreciable economic risk because such trials often suggest far greater potential for a candidate species than is ultimately realised (Malcolm, 1997). Early trials typically contain relatively small numbers of individuals which are likely to escape the pest and disease problems that may affect large scale plantations. Moreover, early trials tend to be grown on sites that are well tended, are of high fertility and are well sheltered from exposure. If the range of environmental conditions covered by initial trials is limited and unrepresentative, this will not provide the data needed to prevent inappropriate planting and can lead to costly failures. This is exemplified by Corsican pine in Britain which, before its limitations were known, was established on north facing slopes and inland sites north of a line between the Humber and the Mersey. These plantations were destroyed by the pathogen *Gremmeniella abietina* (Lagerberg) Morelet which damages trees that are under stress due to lack of winter sun-shine (Read, 1968).

For novel exotics there is also typically a lack of knowledge about adaptive genetic variation across the natural range, data which are provided by multi-site provenance tests comprising material from a wide range of native environments, and are vital for choosing appropriate seed sources for introduction (Zobel et al., 1987). Possession of this knowledge can mean the difference between success and failure. Provenance trials of Douglas fir in Britain demonstrated that seed must be sourced from populations west of the Cascade mountain range in North America to ensure that the species is not damaged by the needle cast fungus *Rhabdoctline pseudotsugae* Syd., (1922) (Lines and Aldhous, 1961). Without this knowledge, use of inappropriate seed sources from interior British Columbia would have led to plantation failure and the erroneous inference that the whole species was unsuitable for introduction to Britain. Provenance trials should ideally be run over as much of the rotation as is practical if costly mistakes are to be avoided. A cautionary example is that of lodgepole pine. For this species, south coastal origins were recommended for planting of upland sites in Britain on the basis of performance in provenance trials at year six. Midway through the rotation, plantations of this provenance suffered catastrophic damage by wet snow, making the trees un-harvestable (Lines, 1966).

A third element of economic risk associated with novel exotics is that there is often a lack of suitable seed sources from which to grow planting stock. In the absence of data from provenance trials, robust recommendations cannot be made about where seed should be sourced. If there are difficulties with collecting from natural populations, it may be necessary to recommend sourcing seed from stands within the introduced range that are of unknown origin. This increases the risk of failure because home grown stands may have been established from seed of few parents, and offspring from such stands are likely to lack genetic variation and possess low fitness due to expression of inbreeding depression (Sorensen and Miles, 1982). Lines et al. (1967) cite the example of a British plantation of Douglas fir derived from seed of two parents which produced inbred offspring with a high number of

deformities. There is also anecdotal evidence that British stands of coast redwood, which may be used for seed collection, have been founded from very few parents (Silvifuture, 2018). Seed sourced from either of these two stands would be wholly unsuitable for generating resilient forests capable of future adaptation, and performance of the stock derived from them would provide an unrealistic picture of the potential of the respective species in Britain.

Another perspective on additional economic risks associated with planting novel exotic species comes from an historical overview of the Forestry Commission's species introduction programme in Britain (MacDonald et al., 1957). Since the 1920s, over 110 exotic conifer taxa have been grown in demonstration plots, and on the basis of their performance 50 candidate exotic conifer species (equivalent at that time to novel exotics) were identified as showing promise. These have been included in species and, in some cases, provenance trials on a wide range of site types. At the end of the trials only ten of these 50 candidate exotic species have so far proved to merit a place in British commercial forestry (Lines, 1987). Of these, only one (Sitka spruce) possesses the ecological attributes that allow widespread utilisation with minimal tending in the difficult upland and marginal sites generally available for planting (Malcolm, 1997). Among the remaining species with considerable commercial potential but more exacting site requirements and more demanding control of browsing and weed growth, a number are compromised by poor wood quality and/or susceptibility to exposure (Wilson, 2011). Furthermore three of these exotic species are currently threatened by diseases which have only become apparent since widespread planting of the species; Corsican pine and lodgepole pine by *Dothistroma* needle blight, and Japanese larch by sudden larch death caused by *Phytophthora ramorum* (Werres et al., 2001) (Brasier and Webber, 2010; Brown and Webber, 2008).

The arguments above indicate that using novel exotics rather than native or well-established exotic species entails substantially increased economic risks. This conclusion is supported by the experience in New Zealand, where between 1925 and 1935 a range of untested exotics was used to diversify a plantation forestry industry reliant on radiata pine (*Pinus radiata* D.Don). This policy proved to be an economic failure (Burdon, 2001). However, given the known limitations of native and well-established exotic species in Britain, there remains a strong argument for introducing a limited range of carefully chosen novel exotic species into commercial forestry, but only after conducting thorough species and provenance trials (Wilson, 2011). The recently established large scale, multi-site species and provenance trial REINFORCE, which is testing performance of over 30 novel exotic species throughout the Atlantic seaboard region of Europe, including Britain, represents a welcome initiative to address this issue (Prieto-Recio et al., 2012). An integral part of this 'response preparation' should be the establishment of stands of each novel exotic in Britain from documented seed sources using an adequate diversity of genotypes, so that they can subsequently be used as seed sources for widespread planting if these species perform successfully in trials (Burdon, 2001). Such a response preparation policy is currently being pursued in New Zealand, where species such as coast redwood, which initially proved a failure in the absence of adequate testing, are being thoroughly reassessed for their potential with appropriate multisite provenance trials (Meason et al., 2016). Given the financial investment needed to conduct a thorough programme of trials for these so-called 'contingency species', a rigorous selection process is essential to ensure resources are directed at those taxa with the greatest likelihood of success.

In terms of commercial conifer production in Britain this process of narrowing down appropriate candidate species is well underway. Comprehensive literature reviews have been compiled (Savill, 2015; Savill and Mason 2015; Savill et al., 2017a, 2017b; Wilson, 2011; Wilson et al., 2016) and, where they exist, analyses of preliminary species trials and limited provenance experiments have been published (Kerr et al., 2015a, 2015b). These data have been supplemented by anecdotal information on small scale *ad hoc* plantings of the candidate

species in the U.K., and preliminary assessments of wood quality and utilisation. However, this level of critical scrutiny is still to be applied to the wider lists of novel exotics proposed for future planting by [Natural Resources Wales \(2017\)](#) and [Forestry Commission England \(2018b\)](#). As an example, five novel exotic species listed as candidates for increasing species diversity (western white pine (*Pinus monticola* Douglas ex D. Don, eastern white pine (*P. strobus* L.), maritime pine (*P. pinaster* Aiton), radiata pine and lenga (*Nothofagus pumilio* (Poepp. & Endl.) Krasser) are known to suffer from serious disease problems already present in Britain ([Table 1](#)). Indeed, planting of both western and eastern white pine was abandoned in Europe at the beginning of the twentieth century as a consequence of their destruction by white pine blister rust (*Cronartium ribicola* J.C. Fisch.) ([Hummer, 2000](#)), and subsequent attempts to grow the species commercially have resulted in failure.

4.1.2. Forests managed for conservation

As we have emphasised above, strong arguments for species replacement under climate change apply to the commercial sector of forestry where productivity is threatened, and silvicultural change is needed. However in situations where the primary objective of management is biodiversity conservation, loss of productivity is not a criterion for species replacement, and should not be used to argue for introduction of novel exotics. Replacement of native tree species is only appropriate if climate model projections suggested that native tree populations can no longer be sustained. Failing to distinguish between commercial and conservation criteria for species replacement can lead to policy confusion.

This potential for policy confusion is nicely illustrated by considering the interpretation of widely cited analyses of climate change impacts on British forests by [Broadmeadow et al. \(2009\)](#) and [Ray et al. \(2010\)](#). They reported that by 2080 conditions in Britain will be 'marginal' or 'unsuitable' for a number of native species. Interpreted uncritically these results give the impression that populations of such native species will be unsustainable in 2080, and will need to be replaced as a consequence of climate change, even where the management objective is conservation. However it is vital to realise that in this context the 'marginal' or 'unsuitable' classifications derived from the ESC model relate only to a measure of commercial performance, the productivity of the native species relative to its maximum possible productivity under present conditions ([Pyatt et al., 2001](#)). This does not imply that the species will be unable to sustain populations or support associated biodiversity by 2080. The term "suitability" in this context is a measure of silvicultural appropriateness, rather than ecological status, though practitioners may well not be aware of this. This difference in usage is well illustrated by the case of sessile and pedunculate oaks which are classified as productively 'marginal' under present climatic conditions in northwest England ([Ray et al., 2010](#)). However in conservation terms these species are currently very successful in this region. Indeed they are dominant components of many native woodlands and support substantial associated biodiversity ([JNCC, 2017](#)).

A more appropriate criterion for deciding whether a native tree species managed for conservation should be replaced at a site on the grounds of climate change is whether the future climatic conditions it is predicted to experience will lie within or outside the climate envelope of that species. For the vast majority of Britain's native tree species, the projected climates at their current sites in 2080 remain well within their present climate envelopes. Indeed the potential ranges of some species currently limited in Britain by low temperatures e.g. small-leaved lime (*Tilia cordata* Mill.) and hornbeam, are predicted to be much larger in 2080 than at present ([Broadmeadow et al., 2009](#)). This is because many tree species in Britain are at the northern edges of their climatic distributions, with the majority of their populations found much further south in continental Europe. Thus all except extreme boreal native tree species such as dwarf birch (*Betula nana* L.) have the potential to accommodate climate changes projected for 2080. If they are managed primarily for biodiversity conservation rather than timber

production, there is therefore no argument to support their imminent replacement on the grounds of inability to cope with climate change.

4.2. Increasing the resilience of forests

One of the most widely used justifications for the introduction of novel exotic species is that the resulting increase in species diversity will confer on the forest an increase in resilience to pests and pathogens. The argument runs that if there is some fixed probability of damage to any one species, then the risk to the forest as a whole will be lower if the portfolio of species is expanded by introducing novel exotics; the more species, the lower the proportion of forest that is affected when a damaging species-specific event occurs. This argument is based on two critical assumptions; that the probability of a damaging event is the same for existing species and novel exotics; and that the presence of novel exotic species does not affect the probability of damage to existing species. We now have evidence from over a century of exotic species use in forestry in Britain and elsewhere in the world, to assess the validity of these assumptions.

When tree species are introduced into an exotic location they are removed from interaction with their natural co-evolved pests and diseases. Release from enemy pressure results in an initial reduction in probability of damage to the exotic species, and can mean an initial increase in productivity in the new location ([Keane and Crawley, 2002](#)). However, the exotic is now in an environment containing native pests and pathogens, and it is usually not long before these native pests and pathogens transfer onto the exotic species ([Boyce, 1941; Burgess and Wingfield, 2017; Ennos, 2015; Wingfield et al., 2015](#)). This process is most likely and most rapid where the exotic is closely related to a native tree species ([Gilbert and Webb 2007; Gilbert et al. 2012](#)). If the exotic species has not been thoroughly tested, and is under stress due to inappropriate planting in an environment to which it is not well adapted, it is likely to be particularly vulnerable to native pathogens which would not normally cause significant damage to well-adapted native species ([Schoeneweiss, 1981](#)). Furthermore, since the exotic species will not previously have encountered the native pests and pathogens, it may suffer from enhanced levels of damage as a consequence of lack of co-adaptation ([Thompson, 2005](#)). The result may be an epidemic of the native pest or pathogen on the exotic tree species.

An example of such an epidemic of native pathogens moving onto an exotic species is provided by the shoot pathogen *Gremenniella abietina*, endemic and not particularly damaging on Scots pine in Sweden, but causing widespread destruction of Swedish plantations of the extensively planted exotic lodgepole pine ([Karlman et al., 1994](#)). Transfer of native insect herbivores from native tree species to related exotics may also take place, as evidenced by pine beauty moth, which is endemic and not problematic on Scots pine in Britain, but causes pest outbreaks and damage when it transfers onto exotic lodgepole pine plantations in Scotland ([Heritage, 1997](#)).

Not only are novel exotics likely to be more vulnerable than native species to native pests and pathogens, their importation can also facilitate the inadvertent introduction of the pests and pathogens which they host in their native range. Overwhelming evidence from across the globe demonstrates that after an initial enemy free period, exotic trees are eventually colonised by pests and pathogens from their native range as a result of long distance transport ([Boyce, 1941; Burgess and Wingfield, 2017; Wingfield et al., 2015](#)). Even the strongest biosecurity measures may not be effective against this, as spores of pathogens can be carried many thousands of miles in air currents. The risk of infection by this means would seem likely to increase as a species is more widely planted; whilst spores may be unlikely to be transferred to a few specimens in arboreta, plantations covering many square kilometres present a larger target for colonisation. In exotic plantations, these may cause more damage than is found in the native range either due to environmental conditions that are favourable to the pathogen, or to stress imposed on the exotic tree due to poor adaptation to its new

planting site.

This situation is exemplified by the case of *D. septosporum* which causes little damage to radiata pine in its native range, but can cause substantial economic losses where it has been inadvertently introduced into radiata pine plantations in the southern hemisphere (Gibson, 1972). In New Zealand radiata pine remains the most important commercial timber species despite the presence of *D. septosporum*, but this has come at the cost of substantial investment in resistance breeding programmes, changes in silviculture, and widespread spraying of copper based fungicides (Bulman et al. 2016). Current estimates of the cost of *D. septosporum* to New Zealand forestry remain at €14million/ annum despite these measures (Meason and Mason, 2014). In Britain the larch canker pathogen (*Lachnellula wilkommii* (Hartig) Dennis), introduced with its host European larch, led to severe cankering of this exotic, especially where alpine provenances ill-adapted to the oceanic climate of Britain were grown (Buczacki, 1973). More recently the lodgepole pine race of *D. septosporum*, accidentally transferred from North America to Scotland during the introduction of lodgepole pine (Mullett et al. 2017; Piotrowska et al., 2018), has caused such severe damage to plantations that large areas of salvage felling have been necessary, and for this reason there is currently a moratorium on planting lodgepole pine in Britain (Brown et al., 2012; Edwards, 2017).

The examples above clearly illustrate that when exotic tree species are introduced and widely grown, this also facilitates the establishment of their pathogens. If an introduced exotic is closely related to a native tree species, there is then the potential for transfer of the exotic pathogen onto the native host. The effects of exotic pathogens are often much more damaging than those of native pathogens because there is no history of co-evolution (Thompson, 2005). A recent example which illustrates this process involves the widespread planting of exotic Corsican pine in the UK which has facilitated the introduction of a new race of *D. septosporum* from continental Europe (Piotrowska et al., 2018). This pathogen has spread north by way of susceptible Corsican pine plantations and is now infecting Scots pine in native pinewoods apparently causing more serious damage than the native race of the same pathogen (Perry et al., 2016a, 2016b). Introduction of exotic tree species into the range of related native species has also been the ultimate cause of the devastating pandemics of chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) and white pine blister rust in North America, and Dutch Elm disease and ash dieback in Europe (Anagnostakis, 1987; Gibbs, 1978; Gross et al., 2014b; Hummer, 2000).

We can conclude that, from worldwide experience of practising exotic forestry for more than a century, the introduction of novel exotic species, far from increasing resilience, can often lead to very serious pest and pathogen problems (Boyce, 1941; Wingfield et al., 2015). Relief of exotic species from disease pressure in novel environments is likely to be a short-lived phenomenon, which may cease when pathogens transfer from native hosts and/or those from their native range are subsequently introduced, or arrive later through natural means. Pest and pathogen damage to novel exotic species is likely to be higher than to their native counterparts, especially in the absence of thorough species and provenance trials. Moreover, where novel exotics are closely related to existing species in the forest, their presence is likely to increase the risk of damage to these native species.

4.3. Supporting biodiversity associated with threatened native species

Following the invasion of exotic pests or pathogens to which a native tree species is susceptible, there are frequently calls to replace the native with a related exotic species possessing similar ecological attributes but exhibiting resistance e.g. Anagnostakis (1987), Buggs (2012), Stone (2013). The stated objective in such cases is to retain the forest structure and support the biodiversity associated with the threatened species. If the exotic concerned has not been thoroughly assessed in species and provenance trials, this policy carries economic risk, as we have argued above. The fact that the introduced species is closely

related to the native species further adds to this risk, because, if under stress due to poor adaptation to novel conditions, the exotic species is likely to be particularly vulnerable to native pathogens. In addition the introduced exotic is likely to provide a conduit for entry of additional exotic pests and pathogens capable of further damaging the native species, reducing its prospects for evolving resistance to the original exotic pathogen.

The risk to the native species is likely to be exacerbated if the exotic tree proves successful and occupies the niche of the native species. Native individuals which possess some resistance, but less than that possessed by the introduced exotic are likely to be outcompeted, hindering the evolution of resistance in the native tree population and reducing its prospects for survival (Ennos, 2015). The power of more resistant species to drive susceptible species to extinction in the presence of a damaging pathogen is seen in California coast redwood forests invaded by the exotic pathogen *Phytophthora ramorum*. Here, high inoculum production by relatively resistant bay laurel (*Umbellularia californica* (Hook. & Arn.) Nutt.) is driving the loss from the community of less resistant tan oak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S.H.Oh) (Cobb et al., 2010).

In the British context, a possible adaptive response to the introduction of the ash dieback fungus *Hymenoscyphus fraxineus* affecting native *Fraxinus excelsior* would be the introduction of an exotic congener resistant to the pathogen. Four novel exotics (*F. ornus* L., *F. americana* L., *F. pennsylvanica* Marshall and *F. mandschurica* Rupr.) were considered as possible candidates by Broome and Mitchell (2017) who pointed out that all these species lack preparatory species and provenance testing and therefore carry a risk of establishment failure. Although these species suffer less damage from *H. fraxineus* than *F. excelsior*, three of the four are tolerant rather than immune to the disease and produce apothecia and spores on fallen leaves (Nielsen et al., 2017). Thus, if these species did successfully establish, their presence would be likely to generate further pathogen pressure on native *F. excelsior*, hasten the loss of native ash in areas where they were planted, and in the long term hinder the evolution of greater resistance in native ash.

It is important to note that several adaptive management strategies other than novel species introduction can be used to mitigate the effect that loss of native species has on ecological function and associated biodiversity. These include management of the proportions of existing native species in the woodland through natural regeneration or planting. In the case of native ash eliminated by the ash dieback fungus, loss of ecological function and associated biodiversity could be reduced by altering the relative proportions of native oak, hazel (*Corylus avellana* L.), beech and aspen (*Populus tremula* L.) present in the community (Broome and Mitchell, 2017).

Another adaptive management strategy that has been suggested for conserving biodiversity relates to the situation where a native species may be lost under long-term climate change. It has been proposed that in these circumstances a related, or unrelated but 'functionally equivalent', exotic species adapted to future predicted climatic conditions should be planted (Stone, 2013). The first objection to this proposal is that the notion of a 'functionally equivalent' species that is not closely related to the affected species is ecologically unsound. Whilst a distantly related species may occupy the same physical niche as a native species, it is highly unlikely to offer a similar combination of traits such as bark pH and roughness, litter and nutrient cycling or shade regime. It is also unlikely to harbour the same community of co-adapted organisms, such as endophytes or epiphytes, or to develop the same community of soil microbiota, therefore functioning as a poor ecological substitute (Rodriguez et al., 2009). A further practical difficulty with implementing this policy is that there is considerable uncertainty in predicting future climatic conditions over the long time scales involved, and in identifying related exotic tree species that would be adapted to those conditions.

A number of these criticisms apply to the suggestion that the exotic

ponderosa pine (*Pinus ponderosa* Douglas ex C.Lawson) should be planted now in native Scots pinewoods in Scotland (Stone, 2013). The idea is that this will ensure the presence of a population of pine trees 400 years hence (after Scots pine has disappeared following climate change) that will support native biodiversity associated with veteran pines. Notwithstanding the objection that *P. ponderosa* is highly susceptible to *Dothistroma* needle blight (Gilmour and Noorderhaven, 1969), which is now a serious problem in native pinewoods, the few species trials conducted with this exotic suggest that it would not establish successfully in native pine sites under present climates, and therefore would not be present to fulfil an ecological role 400 years in the future (MacDonald et al., 1957).

4.4. Wider ecological effects of novel exotics on native forests

As we have emphasised in our outline of British forestry, commercial production and conservation objectives are often conducted in close proximity, and management policies pursued in one forestry sector can have major impacts on other sectors. Holistic management of British forests must therefore consider the effects of novel exotic introduction not only on the forest sector for which they are proposed, but across the spectrum of forest types within the landscape. We have already demonstrated that use of exotics in the commercial sector can have an indirect impact on native woodlands managed for conservation through damage caused by shared pests and pathogens. Introduced exotics can also have direct ecological impacts if, through seed dispersal outside their area of introduction, they invade native woodlands. Problems caused by invasive tree species in native forests are found worldwide and are of increasing severity (Rejmanek and Richardson, 2013; Richardson and Rejmanek, 2011). In Europe, four of the eighteen worst invasive terrestrial plants are trees (*Acacia dealbata*, *Ailanthus altissima*, *Prunus serotina*, *Robinia pseudoacacia*) (DAISIE, 2018). In Denmark, problems are so serious that there are eradication programmes for *Prunus serotina* and *Pinus mugo*, both of which have become invasive since they were introduced over a century ago (Krumm and Vítková, 2016). The effects on native forests of exotic tree invasion include changes in decomposition rates (Ashton et al., 2005), plant community composition (Halarewicz and Żolnierz, 2014) and a diversity of ecosystem functions (Aerts et al., 2017).

In order to appreciate the potential ecological impacts of invasive tree species in the context of British forestry, it is important to outline the characteristics of British native woodlands that confer on them their special conservation value. British woodlands have fewer native species of trees, shrubs and herbaceous plants than their continental European counterparts as a result of Britain's island status, the global trend for fewer species at high latitudes, lags in colonisation from refugia following the last Ice Age (Ingrouille, 1995), and past management (Anderson, 1967; Côté et al., 2004; Watts, 2006). In particular they contain few of the more shade-tolerant tree species, especially in Scotland. As a consequence, the realised niche of many of the tree species in Britain is much wider than for the same species on the continent. For instance, Scots pine occupies areas of high oceanicity in the west of Scotland that would otherwise be occupied by Norway spruce if that species was present.

The absence of shade-tolerant species in many woodlands, the wide ecological amplitude of native trees in Britain, and the humid oceanic climate of western Britain has led to the development of associated communities that are both unique to Britain and of high conservation value globally. These comprise species-rich assemblages of ferns, mosses and liverworts, and include both the richest communities of oceanic bryophytes in Europe (Averis et al., 2012) and a correspondingly diverse oceanic lichen flora (Ellis, 2016). British woods are also globally important for vernal herbaceous plants, some of which benefit from the lack of shade tolerant trees. An example is bluebell (*Hyacinthoides non-scripta*) which has the bulk of its global distribution in Britain. In many ways, Britain's lack of tree and shrub species adds to

the conservation value of those that are present, rather than detracting from it.

These attributes of Britain's native forest communities make them particularly prone to invasion and damage by shade-tolerant tree species whose presence can completely change the character of the woodland. This is demonstrated by the effects of introduction of shade tolerant beech, Douglas fir and western hemlock, into broadleaved woodlands in Scotland. Increased shade excludes much of the vascular ground flora, and even the more shade-tolerant native tree species (rowan (*Sorbus aucuparia* L.), hazel) are unable to regenerate under the canopy, with knock-on effects for other species such as epiphytic lichens (Broome and Mitchell, 2017). Indeed the demise of vascular and non-vascular ground flora and epiphytes may lead to total loss of the biodiversity features that give these woodlands their unique conservation value (Scottish Natural Heritage, 2011). These considerations indicate that any introductions of novel exotic tree species in Britain must take into account their potential for invasiveness, recognising that shade tolerant trees are likely to pose the greatest risk to native woodland communities.

In addition to invasion through spread of seed or other propagules from an introduction site, genetic invasion can also occur through hybridisation with related native species. From the conservation viewpoint, this is most serious where the native population is small and vulnerable and may be 'hybridised out of existence' by the introduced species. Centuries of hybridisation between the native crab apple (*M. sylvestris*) and the introduced domestic apple (*M. domestica*), has resulted in 7–39% of wild grown crab apple trees in a range of European countries being hybrids (Cornille et al., 2013, 2014). Work in progress in Scotland and northern England (Worrell et al., 2017) suggests that 25–30% of mature crab apple trees growing in the wild and/or planted in hedgerows are hybrids, with pure populations of *M. sylvestris* restricted to more isolated upland areas. There is good evidence for a similar situation in Canada where the native, but locally rare, red mulberry (*Morus rubra* L.) hybridises extensively with introduced white mulberry (*M. alba* L.). On red mulberry parents, hybrid seeds are replacing seeds of pure red mulberry, leading to gradual reduction in the latter's population size (Burgess and Husband, 2006).

In Britain such problems could occur in black poplar (*Populus nigra* L.), whose population size is currently no more than 7000 individuals. Large scale planting of hybrid poplar (*P. deltoides* W.Bartram ex Marshall × *P. nigra*) in the vicinity of isolated females of black poplar, would lead to the production of backcross individuals with one quarter of their genes coming from the American species *P. deltoides* rather than pure *P. nigra* offspring (Cottrell, 2004). Similar pollen swamping could also occur if hybrid aspen (*P. tremula* L. × *P. tremuloides* Michx.) (Rytter & Stenna, 2005) was planted among native aspen *P. tremula* populations in Scotland, where numbers of female individuals flowering are usually very small, and loss of pure seed through production of hybrids can be ill-afforded (Mason et al., 2002; Worrell, 1995). Since variation in aspen genotype is known to have significant effects on the composition of epiphyte communities (Davies et al., 2014), this would be of concern for conservation more generally. Thus policy on introduction of novel exotics in Britain must also consider their potential for hybridisation with native species (and established exotics), and the possible deleterious consequences that this may have.

5. Summary and conclusions

The primary objective of this paper has been to assess whether there are strong arguments for introducing novel exotic tree species to mitigate the adverse effects of rapid climate change and continued influx of new pests and pathogens, using the particular example of British forestry. Our analysis has shown that there are compelling arguments for limited and targeted species replacement and diversification in the commercial sector of British forestry where timber production is the major aim. A replacement for Sitka spruce is required in the eastern part

of its current range in Britain in response to increases in drought stress under climate change. In addition one or more exotic species possessing shade tolerance are needed in the future, not only to increase the species diversity of plantations, but also to facilitate the widespread implementation of continuous cover forestry and the associated structural diversity that it brings (Kerr, 1999).

In choosing the species to be used for replacement and diversification in the commercial sector, a number of factors need to be taken into consideration. The first is the scale of the economic risk associated with using that species, set against the potential benefits from high production of marketable timber. The second is the probability that use of the species will pose a biosecurity threat. Finally it is essential to determine whether the species is likely to become invasive and cause serious economic and ecological damage in the introduced range. Table 1 lists the novel exotic species that have been proposed for introduction in British forestry and it is instructive to use the data in this table to assess the risks associated with planting them.

Evidence from analysis of historical exotic introductions indicates that the economic risk of using untried exotic species is very high, and that only species that have proved themselves after species and provenance tests, and for which a secure seed source is available, should be recommended for widespread planting. It is clear from Table 1 that the novel exotic species proposed for introduction vary widely in the extent to which they fulfil the criteria outlined above, and this should help to determine the relative risk associated with their introduction on a forestry scale. The prudent course of action is to make use of a native or well-established exotic species until such time as the appropriate research programme for a candidate species is complete, and to introduce that species cautiously so that any problems with larger scale planting can be recognised and the introduction programme modified before too much has been invested in the species.

Our discussion of the resilience of forests to pests and diseases suggests that the greatest biosecurity threat is associated with introduction of exotic species that are closely related to species already present in the introduction site or its vicinity. Given that British commercial forestry is currently heavily reliant on a single species, Sitka spruce, the biosecurity risk to the industry would be raised by the introduction of further exotic spruces which could facilitate introduction of spruce-specific pests and pathogens. Bearing this in mind, it is of concern that one of the novel exotic species currently being considered for introduction into British forestry is oriental spruce, *P. orientalis*, for which there are few forest plots and no provenance tests, and which is known to be highly susceptible to the great spruce bark beetle (*Dendroctonus micans* (Kugelann, 1974)) (Table 1) (Savill et al., 2017b). This beetle is already causing damage on drought stressed Sitka spruce in England and southern Scotland (Forestry Commission, 2012). Similar concerns are associated with the introduction of Serbian spruce, *P. omorika*, which is also being planted commercially (Royal Forestry Society, 2014). In terms of biosecurity risk to broadleaved tree species, the suggestion that bigleaf maple (*Acer macrophyllum* Pursh) and silver maple (*Acer saccharinum* L.) should be planted in England is problematic, given that they are related to non-native but well-established sycamore, *Acer pseudoplatanus*, an increasingly important timber producing species in Britain.

From the viewpoint of native woodlands managed for biodiversity, it is vital to screen the initial list of novel exotics for their invasive potential. As we have indicated, species posing greatest risk are those that possess high shade tolerance. These figure prominently in the list of novel exotic conifers proposed for diversifying Sitka spruce plantations (Table 1), suggesting a conflict between commercial and biodiversity objectives. It has already been found that exotic invasive woody species with high shade tolerance such as beech and rhododendron (*Rhododendron ponticum* L.) are the primary cause of unfavourable conservation status in designated native woodlands in Scotland (Scottish Natural Heritage, 2011). Thus if new shade tolerant conifers are ultimately to be introduced, there is a clear onus on those advocating their introduction,

to demonstrate that the species will not become invasive and damaging to native biodiversity.

On the basis of these considerations, a major recommendation from this review is that there needs to be a fundamental change in attitude to the introduction of exotic tree species into forestry in Britain. Exotic introduction may assist with a well-defined set of problems that are currently faced by the commercial forestry sector as a consequence of rapid climate change and exotic pests and pathogen introductions. However it must be recognised that species introduction brings with it serious risks both to the existing commercial sector and to native woodland biodiversity. Therefore exotic introduction policy must be positioned more firmly within a risk assessment framework where the obligation is on those advocating the introduction of novel exotic species to outline the tangible benefits that will come from introduction, demonstrate that the potential economic, biosecurity and ecological risks have been identified and evaluated, and ensure that all necessary steps have been taken to minimise these risks before any proposed introduction takes place. This is the approach taken by forestry in New Zealand (Burdon, 2001), Canada (Thorpe et al., 2006), Sweden (Felton et al., 2013) and other Nordic countries (Kjær et al., 2013, 2014). With the passing of the Wildlife and Environment Act (Scotland) 2011 the framework for comprehensive regulation of novel exotic introductions is now in place in Scotland (Forestry Commission Scotland, 2015), but such a framework appears to be lacking in England and Wales.

The second major conclusion from our analysis is that in situations where biodiversity conservation is a significant objective, there are no credible arguments for, and many counterarguments against, the introduction of novel exotic tree species. In response to climate change over the next century, the productivity of native British tree species is likely to change, but they will remain within their respective climatic envelopes and continue to support associated biodiversity. There is therefore no immediate need to replace them. The idea that introducing novel exotic species will increase the resilience of native forests in the face of environmental change is shown to be problematic. Indeed, evidence from historical introduction programmes suggests that exotic introduction can decrease the resilience of native woodlands to pests and pathogens. Finally, the idea that novel exotics should be used to replace native species affected by introduced pests and pathogens is unsupported. Introduction of untested exotic species carries a high risk of failure. Furthermore, if establishment of novel exotics were successful, this would be likely to restrict the ability of native species to evolve resistance to the threat organisms, and hasten the demise of these native species. Any strategy for increasing species diversity in native woods should therefore be based on the continued use of native species, working to address situations where native woods have effectively become monocultures due to past management practices.

Finally, novel exotic introduction is far from a panacea for the problems posed by rapid climate change and influx of exotic pests and pathogens. Both in commercial plantations and in native woodlands, the forest tree species in Britain, whether native or introduced, will need to be able to evolve in response to continuing and unpredictable abiotic and biotic environmental change. Silvicultural systems in commercial forestry that enable production populations to evolve (Burdon, 2001), and regeneration systems in native forests that facilitate adaptive genetic change (Cavers and Cottrell, 2015), are likely to be more effective than exotic introductions as management tools for responding to rapid changes in the abiotic and biotic environments of forest trees.

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Appendix A. Supplementary material

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